

# Revision of *Discomesites* and *Estaingia* (Trilobita) from the Lower Cambrian Cymbric Vale Formation, Western New South Wales: Taxonomic, Biostratigraphic and Biogeographic Implications

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The taxonomy of *Discomesites* and *Estaingia* from the Lower Cambrian Cymbric Vale Formation of western New South Wales is revised. *Discomesites* is regarded as a valid subgenus of *Pagetides*. *Pagetides* (*Discomesites*) *fragum* is considered a senior subjective synonym of *P. (D.) lunatulus*. *Pagetides* (*Discomesites*) *spinosus* from the Shackleton Limestone in the Holyoake Range, Transantarctic Mountains, is considered to be a junior subjective synonym of *P. (D.) fragum*. *Estaingia cerastes* from the Cymbric Vale Formation is considered to be synonymous with *Hsuaspis* cf. *H. bilobata* from the Shackleton Limestone. The Cymbric Vale Formation trilobite fauna is of late Early Cambrian (late Botoman) age, equivalent to the *Pararaia janeae* Zone of South Australia, based on correlation of the *Syringocnema favus* archaeocyathan fauna. Absolute ages of recently dated tuffs from the Cymbric Vale and Billy Creek Formations are questioned, based on new information regarding the stratigraphic position of the Cymbric Vale Formation tuff in relation to archaeocyathan and trilobite biostratigraphy. The co-occurrence of *Pagetides* (*Discomesites*) *fragum* and *Estaingia cerastes* in the upper part of the Cymbric Vale Formation and in the Shackleton Limestone represents the first species-level correlation between the Lower Cambrian of Australia and Antarctica using trilobites. The distribution of these trilobite species, in association with the *Syringocnema favus* archaeocyathan fauna, provides supporting evidence that Australia and Antarctica were connected by a continuous carbonate-detrital shelf during the late Early Cambrian (mid-late Botoman), allowing faunal exchange between these regions.

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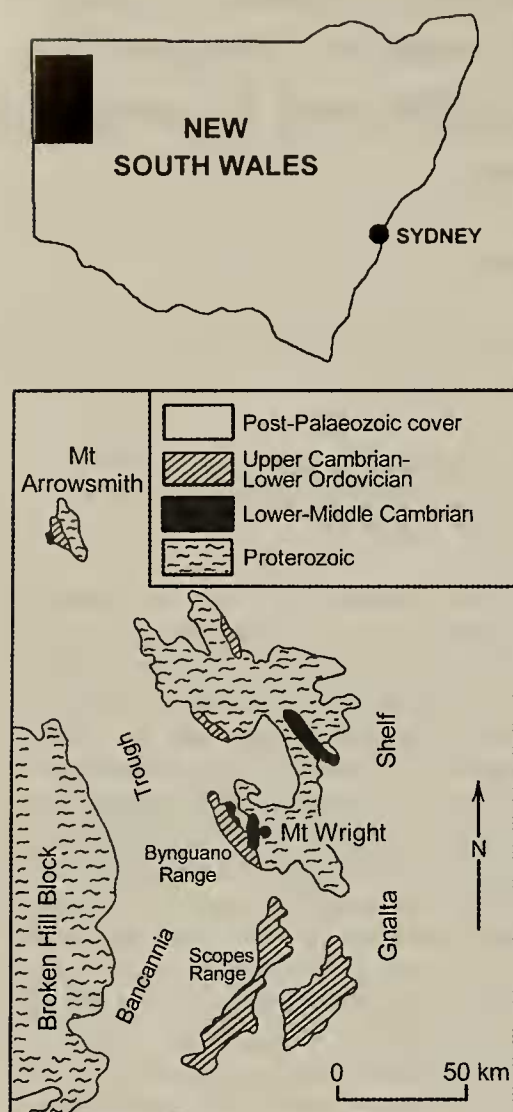
KEYWORDS: Antarctica, Australia, biogeography, biostratigraphy, Botoman, Early Cambrian, geochronology, Gondwana, New South Wales, Trilobita.

## INTRODUCTION

Since the publication of Öpik's (1975b) taxonomic study on the trilobites from the Lower Cambrian Cymbric Vale Formation, several important palaeontological and geochronological studies on the Early Cambrian of Australia and Antarctica, relevant to the Cymbric Vale Formation, have been published (Kruse 1978, 1982; Debrenne and Kruse 1986; Bengtson et al. 1990; Zhuravlev and Gravestock 1994; Palmer and Rowell 1995; Jago et al. 1997; Jenkins et al. 2002). The scope of this study is to revise the taxonomy of two key trilobite taxa from the Cymbric Vale Formation, *Discomesites* and *Estaingia*, as well as review the archaeocyathan biostratigraphy of the

Cymbric Vale Formation and stratigraphic position of a recently dated tuff within the unit, allowing the Cymbric Vale trilobite fauna to be placed in both a biostratigraphic and biogeographic context.

The Cymbric Vale Formation is part of the Lower to early Middle Cambrian Gnalta Group, which crops out in the Mt Wright area of western New South Wales (Fig. 1). The Gnalta Group comprises (in ascending order): the Mount Wright Volcanics, Cymbric Vale Formation and Coonigan Formation. The Lower Cambrian Mount Wright Volcanics and overlying Cymbric Vale Formation are considered to be conformable, based on common archaeocyathan faunas (Kruse 1982). The uppermost beds of the Cymbric Vale Formation are disconformably overlain by the early Middle Cambrian 'first discovery



**Figure 1. Generalised geological map of northwestern New South Wales, showing location of Mt Wright; modified from Shergold et al. (1982, text-fig. 1D).**

limestone' of the Coonigan Formation (Roberts and Jell 1990).

The Cymbric Vale Formation attains a maximum thickness of 1900 m and consists predominantly of interbedded blue, green and grey-white chert and green to brown tuff (Kruse 1982). Archaeocyath-bearing limestone lenses occur throughout the formation and contain two distinct archaeocyathan faunas (Fig. 2): Fauna 1 (L96-L99) occurs in the upper Mount Wright Volcanics and in the lower part of the Cymbric Vale Formation and is assigned an early Botoman age; Fauna 2 (L100-L101) occurs in the upper Cymbric Vale Formation and has been assigned a mid-late Botoman age (Kruse 1978, 1982; Zhuravlev and Gravestock 1994; Kruse and Shi in Brock et al. 2000). The uppermost beds of the Cymbric Vale Formation consist of well-bedded lithic and feldspathic siltstone and sandstone interbedded with impure iron-rich

carbonate rocks with abundant trilobites, molluscs, brachiopods, coelocrinoids and sponge spicules (Öpik 1975b; Kruse 1982; Jago et al. 1997).

The first formal taxonomic study of the Early Cambrian trilobites from the Cymbric Vale Formation was by Öpik (1975b). He recorded the trilobites *Dinesis* aff. *granulosus* (Lermontova), *Estaingia bilobata* Pocock, *Strenax cerastes* Öpik, *Strenax* (*Sematiscus*) *fletcheri* Öpik, *Serrodiscus daedalus* Öpik, *Meniscuchus menetus* Öpik, *Discomesites fragum* Öpik, *Discomesites lunatulus* Öpik and *Pagetia* sp. nov. Öpik (1975b) correlated the Cymbric Vale fauna with Daily's (1956) South Australian faunal assemblages 9, 11 and 12, equivalent to the *Pararaia janeae* Zone of South Australia (Bengtson et al. 1990), and to the Botoman Sanashtyk'gol Horizon of the Altay-Sayan region of Siberia.

Jago et al. (1997) recorded a trilobite faunule from a new locality within the Cymbric Vale Formation, reassigning the species *Estaingia bilobata* Pocock and *Strenax cerastes* Öpik, originally documented by Öpik (1975b), to a single redefined species, *Hsuaspis cerastes* (Öpik), and also described *Redlichia* cf. *ziguiensis* Lin, a taxon previously unknown from the Cymbric Vale Formation. Jago et al. (1997) also suggested that the Cymbric Vale trilobite fauna is of late Early Cambrian (late Botoman) age.

#### BIOSTRATIGRAPHIC IMPLICATIONS

The taxonomic revision herein of *Pagetides* (*Discomesites*) *fragum* Öpik, 1975b and *Estaingia cerastes* (Öpik, 1975b) from the Cymbric Vale Formation of western New South Wales is based on reexamination of Öpik's (1975b) type material plus additional collections housed at Geoscience Australia (Canberra) and provides the first direct interregional correlation between the Lower Cambrian of Australia and Antarctica using trilobites. Palmer (in Palmer and Rowell 1995) described a number of Early Cambrian trilobite assemblages, ranging in age from Atdabanian to Toyonian(?), from the Shackleton Limestone in the Holyoake Range of the central Transantarctic Mountains. One of the Botoman assemblages ('Assemblage 3') contains the taxa *Pagetides* (*Discomesites*) *spinosus* Palmer and *Hsuaspis* cf. *H. bilobata* (Pocock). The synonymy herein of *Pagetides* (*Discomesites*) *spinosus* with *P. (D.) fragum*, and *Hsuaspis* cf. *H. bilobata* with *Estaingia cerastes* permits direct correlation of the trilobite fauna from the uppermost Cymbric Vale Formation with trilobite 'Assemblage 3' from the Shackleton Limestone. Unfortunately, further support for this correlation

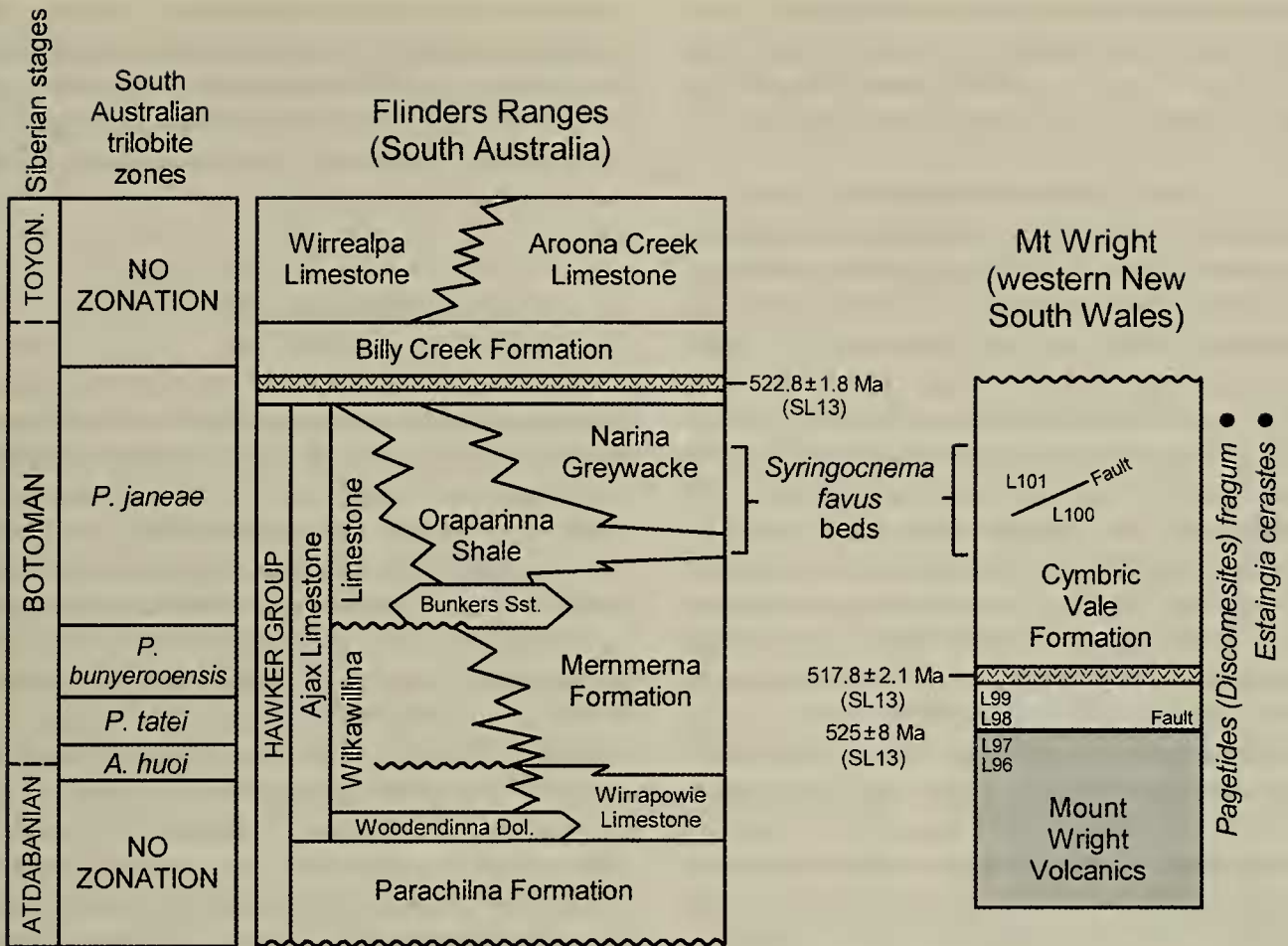


Figure 2. Correlation diagram of the Lower Cambrian successions of Mt Wright (western New South Wales) and the Flinders Ranges (South Australia). L96-L99 represent Fauna 1 and L100-L101 represent Fauna 2 of Kruse (1982). Tuff ages: Billy Creek Formation, 522.8 ± 1.8 Ma (Gravestock and Shergold 2001); Cymbric Vale Formation, 517.8 ± 2.1 Ma (Jenkins et al. 2002) and 525 ± 8 Ma (Zhou and Whitford 1994).

based on similar archaeocyathan faunas from the Cymbric Vale Formation (Kruse 1978, 1982) and the Shackleton Limestone (Debrenne and Kruse 1986) is complicated. Trilobites and archaeocyaths described from the Shackleton Limestone were sampled from different localities in the Holyoake Range; see discussion by Palmer and Rowell (1995:4). Exposed sections of Shackleton Limestone in the Holyoake Range are considerably thick (up to 200 m) and seem to conform to a coherent stratigraphy; however, each section is bounded either by intensely disturbed zones of folding or faulting, or fields of ice or névé (Rowell et al. 1988:399; Rees et al. 1989:343). Sampling of trilobites and archaeocyaths from disparate localities in the Holyoake Range, coupled with the structural complexity of the region, makes correlation between faunas difficult.

Documentation of archaeocyathan faunas from the Cymbric Vale Formation (Kruse 1978, 1982), and the development of a preliminary Early Cambrian archaeocyathan biozonation for Australia (Zhuravlev and Gravestock 1994), has allowed for the

correlation of the Cymbric Vale Formation with the Lower Cambrian succession in South Australia. As noted by Kruse and Shi (in Brock et al. 2000), Fauna 2 from the upper Cymbric Vale Formation can be correlated with the mid-late Botoman *Syringocnema favus* beds of the Adelaide Geosyncline (Fig. 2), based on five co-occurring species. Zhuravlev and Gravestock (1994, Table 2) have recorded the *S. favus* beds occurring in the Koolywurtie Member of the Parara Limestone on Yorke Peninsula in the Stansbury Basin, and in the upper Ajax Limestone (Ajax Mine and Mount Scott Range) and upper Wilkawillina Limestone (Wilkawillina Gorge) in the Arrowie Basin. Trilobites from coeval beds in the Flinders Ranges (Arrowie Basin) are representatives of the *Pararaia janeae* Zone (Bengtson et al. 1990). While species-level correlation between the Cymbric Vale and Flinders Ranges trilobites is not possible, generic similarities are evident with the occurrence of *Serrodiscus* and *Estaingia* in both areas (Öpik 1975b; Bengtson et al. 1990). Since the Cymbric Vale trilobite fauna occurs in the uppermost part of the formation,

stratigraphically above archaeocyathan Fauna 2 (= *S. favus* beds), it is equivalent to the *Pararaia janeae* Zone (*sensu lato*) or possibly even younger, thus supporting the late Botoman age suggested by Jago et al. (1997).

A dated felsic tuff from the Cymbric Vale Formation was recently re-calculated by Jenkins et al. (2002) using the SL13 U-Pb SHRIMP method. The tuff was originally collected by Zhou (1992) and subsequently dated by Zhou and Whitford (1994), yielding an age of  $525 \pm 8$  Ma (SL13). However, Jenkins et al. (2002) produced an age of  $517.8 \pm 2.1$  Ma. Unfortunately, neither publication citing the age of the Cymbric Vale tuff (Zhou and Whitford 1994; Jenkins et al. 2002) provided information about the stratigraphic position of the tuff horizon, especially in regard to the local biostratigraphy. However, Zhou's (1992) unpublished PhD thesis does provide an Australian standard national grid reference for the dated sample (i.e., 6332E; 65498N). Based on this grid reference and mapping by Zhou (1992, map 7) and Kruse (1982, text-Fig. 2), the dated tuff appears to have been collected in the vicinity of, or possibly stratigraphically above, Kruse's (1982) localities L98 and L99 in the lower Cymbric Vale Formation (Fig. 2).

In light of the known stratigraphic position of the dated Cymbric Vale tuff, there appears to be an age discrepancy of dated tuffs from the Cymbric Vale Formation and the lower Billy Creek Formation (Flinders Ranges), based on the correlation of the *Syringocnema favus* beds. Gravestock and Shergold (2001) reported a SHRIMP age of  $522.8 \pm 1.8$  Ma from a tuff within the lower Billy Creek Formation using the same standard (SL13) used by Jenkins et al. (2002) to re-calculate the Cymbric Vale tuff. This means that the "older" (522.8 Ma) Billy Creek Formation tuff occurs stratigraphically above the *Syringocnema favus* beds in the Flinders Ranges, and the "younger" (517.8 Ma) Cymbric Vale tuff occurs stratigraphically below archaeocyathan Fauna 2 (= *S. favus* beds) in western New South Wales (Fig. 2). This discrepancy implies that the age of the tuff horizon in the Cymbric Vale Formation or Billy Creek Formation is erroneous, or perhaps both ages are incorrect. This age discrepancy may be related to the standard used, since the reliability of the SL13 standard has been questioned in recent years (see Jago and Haines 1998 for detailed discussion). It is interesting to note that the original age of the Cymbric Vale tuff of  $525 \pm 8$  Ma, calculated using the SL13 standard (Zhou and Whitford 1994; Jago and Haines 1998), is more in accord with the archaeocyath and trilobite biostratigraphy and the age of the Billy

Creek Formation tuff. Furthermore, ages of the Cymbric Vale and Billy Creek Formation tuffs using the alternative QGNG standard yield dates of  $531.8 \pm 8$  Ma and  $529.6 \pm 1.8$  Ma respectively (Jago and Haines 1998), that better conform to archaeocyath and trilobite biostratigraphy.

#### BIOGEOGRAPHIC IMPLICATIONS

Jago (in Brock et al. 2000) noted that Early Cambrian trilobites from Australia have close faunal ties with other regions of East Gondwana, such as Antarctica, South and North China, Iran and India. However, Jago also demonstrated that faunal links with distantly separated palaeogeographic regions such as western Gondwana (e.g. Morocco), Laurentia and Siberia are not uncommon. In discussing the biogeographic patterns of Early Cambrian trilobite faunas from Antarctica, Palmer (in Palmer and Rowell 1995:5) observed that 'Antarctic faunas do not show any consistent similarity to faunas from any one geographic region of the rest of Gondwana'. This appears to be true for any palaeogeographic region when treating Early Cambrian trilobite faunas as a whole, although by closely observing faunal assemblages from specific time intervals, whether they be zones or stages, distinct biogeographic patterns often emerge (for example, see Theokritoff 1979, 1985; Burrett and Richardson 1980; Alvaro et al. 2003). Moreover, Alvaro et al. (2003:17) have commented that in the Lower Cambrian 'the ideal of a global biostratigraphy and palaeobiogeography suffers from both a relatively limited diversity of trilobites and their pronounced endemism. Furthermore, the distribution of trilobites is...strongly controlled by facies, so that even a precise interregional correlation is difficult'.

The occurrence of *Pagetides* (*Discomesites*) *fragum* and *Estaingia cerastes*, in addition to the *Syringocnema favus* archaeocyathan fauna, in the Cymbric Vale Formation (Gnalta Shelf) and the Shackleton Limestone (Holyoake Range) provides supporting evidence that a continuous continental shelf connected southeastern Australia and the Transantarctic Mountains during the Early Cambrian (Rowell and Rees 1991; Courjault-Radé et al. 1992; Wrona and Zhuravlev 1996; Veevers et al. 1997; Brock et al. 2000; Veevers 2000). The palaeogeographic distance between the Gnalta Shelf and the Holyoake Range is estimated to be around 2500 km (Brock et al. 2000, Fig. 8), although the shelf may have extended as far as King George Island, implying a length of over 6500 km. Courjault-Radé et al. (1992,

Fig. 2) have suggested that throughout the Early Cambrian, and indeed the Middle and Late Cambrian, a continuous carbonate-detrital shelf connected Australia and Antarctica. The widespread dominance of the *Syringocnema favus* fauna in Australia and Antarctica during the mid-late Botoman coincides with a global high sea level, allowing faunal exchange between these regions (Zhuravlev and Gravestock 1994; Wrona and Zhuravlev 1996; Gravestock and Shergold 2001). This strong faunal link between Australia and Antarctica during the Botoman is also supported by conspecific occurrences of small shelly fossils (SSF), such as *Eiffelia araniformis* (Missarzhevskiy), *Chancelloria racemifundis* Bengtson, *Halkieria parva* Conway Morris, *Dailyatia ajax* Bischoff, *Lapworthella fasciculata* Conway Morris and Bengtson, *Hyolithellus micans* (Billings), *Hyolithellus filiformis* Bengtson, *Byronia? bifida* Wrona, and *Aetholicopalla adnata* Conway Morris, from glacial erratics of King George Island, Antarctica (Wrona 2004) and the Parara, Wilkawillina and Ajax Limestones and Kulpara and Mernmerna Formations in South Australia (Bengtson et al. 1990; Gravestock et al. 2001).

The carbonate-detrital shelf connecting Australia and Antarctica may have persisted until at least the early Late Cambrian (Idamean), based on other conspecific occurrences of benthic, shelf-dwelling polymerid trilobites and other biotas. For example, Holmer et al. (1996) described an Early Cambrian lingulate brachiopod faunule, containing *Eoobolus* aff. *E. elatus* (Pelman), *Karathele napuru* (Kruse) and *Vandalotreta djagoran* (Kruse), from the glacial erratics of King George Island, Antarctica. These same brachiopod species have been documented from the Toyonian (latest Early Cambrian) Wirrealpa and Ramsay Limestones in South Australia (Brock and Cooper 1993; Gravestock et al. 2001), and early Middle Cambrian units in the Northern Territory: Tindall Limestone, Daly Basin (Kruse 1990); Montejinni Limestone of the Wiso Basin and Gum Ridge Formation of the western Georgina Basin (Kruse 1998); and the Top Springs Limestone, northern Georgina Basin (Kruse 1991). The latest Middle Cambrian (*Glyptagnostus stolidotus* Zone) trilobite species *Rhodonaspis longula* Whitehouse has been recorded from the Georgina Limestone, Glenormiston, Queensland, Australia (Whitehouse 1939; Öpik 1963) and in the Spurs Formation, Northern Victoria Land, Antarctica (Jago and Cooper 2001). Furthermore, the early Late Cambrian (Idamean) trilobite species *Protemnites magnificans* Shergold and Webers has been recorded from the Dolodrook River limestones, eastern Victoria, Australia (Paterson

and Laurie 2004) and from the Minaret Formation, Ellsworth Mountains, West Antarctica (Shergold and Webers 1992).

The position of Australia and Antarctica during the Cambrian, coupled with the persistence of carbonate deposition in Australia and Antarctica throughout the Cambrian, indicates that these regions remained within the tropical Carbonate Development Zone ( $30 \pm 5^\circ$  north and south latitudes) (McKerrow et al. 1992; Courjault-Radé et al. 1992; Brock et al. 2000; Li and Powell 2001). Hence migration of trilobite species between Australia and Antarctica was not inhibited by a latitudinal thermocline during the Cambrian. However, this does not explain the lack of conspecific occurrences of Early Cambrian trilobites between Australia and Antarctica, although one may argue that a paucity of data from Antarctica could be responsible. Moreover, there is a distinct absence of conspecific occurrences between western New South Wales (Gnalta Shelf) and South Australia (Adelaide Geosyncline). One possible explanation for the absence of conspecific occurrences of Early Cambrian trilobites between South Australia and Antarctica is the presence of a tectonic barrier during this time, i.e., the Kanmantoo Trough (Haines and Flöttmann 1998; Flöttmann et al. 1998). The Early Cambrian palaeogeographic relationship between the eastern Arrowie Basin (eastern South Australia) and the Gnalta Shelf (western New South Wales) is, however, poorly understood. Various studies (e.g., Cook 1988; Gravestock and Hibburt 1991; Scheibner and Basden 1998; Zang 2002) have inferred connection between the eastern Arrowie Basin and the Gnalta Shelf via a common seaway. While correlation of the *Syringocnema favus* beds provides supporting evidence for a connected seaway during the late Early Cambrian (mid-late Botoman), there may have been some form of geographic barrier that inhibited trilobite migration between these regions. Firstly, it is important to note that the Cymbric Vale Formation trilobites occur stratigraphically above the *S. favus* beds and that during their temporal separation the palaeogeography between the eastern Arrowie Basin and the Gnalta Shelf may have altered significantly, severing ties between these regions. There are two possible palaeogeographic barriers that may have hindered migration of Early Cambrian trilobites between the eastern Arrowie Basin and the Gnalta Shelf: (1) the Mount Wright Volcanic Arc situated immediately to the west of the Gnalta Shelf; and (2) an inferred trough situated to the west of the Mount Wright Volcanic Arc (Scheibner and Basden 1998, Fig. 14.6). A small outcrop of the Lower-Middle Cambrian Teltawongee beds, considered by

Mills (1992) to be coeval with the Gnalta Group, occurs at the northern end of the Mount Wright Block at Nundora. The Teltawongee beds are thought to have been deposited as a turbidite slope-trough facies (Mills 1992). Scheibner and Basden (1998) suggested that the Teltawongee beds might extend beneath the large thickness of Devonian sediments within the Bancannia Trough, situated to the west of the Gnalta Shelf. This inferred trough would have created an oceanic barrier between the eastern Arrowie Basin and the Gnalta Shelf.

Wrona (2004) observed that Lower Cambrian horizons in Australia and Antarctica that contain very similar faunas correspond with transgressive episodes that occurred during the early Botoman, late Botoman and middle Toyonian (Gravestock and Shergold 2001; Gravestock et al. 2001). Wrona (2004:52) suggested that several isolated basins might have existed along the East Antarctic craton and that those basins 'connected only during the most prominent transgressions, thus allowing faunal exchange'. Alvaro et al. (2003) suggested that species migration of Cambrian trilobites along the western Gondwanan margin coincides with transgressive episodes and subsequent connection of neighbouring platforms. This also appears to have been the case in influencing trilobite migration patterns along the eastern Gondwanan margin, especially between Australia and Antarctica.

#### SYSTEMATIC PALAEOONTOLOGY

Specimens come from the Commonwealth Palaeontological Collection (prefix CPC) housed at Geoscience Australia, Canberra.

Order AGNOSTIDA Salter, 1864  
 Suborder EODISCINA Kobayashi, 1939  
 Family EODISCIDAE Raymond, 1913  
 Genus PAGETIDES Rasetti, 1945

#### Type species

*Pagetides elegans* Rasetti, 1945, Early Cambrian, Sillery Formation, Quebec, Canada.

Subgenus DISCOMESITES Öpik, 1975b

#### Type species

*Discomesites fragum* Öpik, 1975b, Early Cambrian, Cymbric Vale Formation, Mt. Wright, western New South Wales, Australia.

#### Discussion

Palmer's (in Palmer and Rowell 1995) treatment and diagnosis of *Discomesites* as a subgenus of *Pagetides* is supported here.

*Pagetides (Discomesites) fragum* Öpik, 1975b  
 Fig. 3A-K, Fig. 4A-J

*Discomesites fragum* Öpik, 1975b:32, Pl. 5, Figs 1-8.

*Discomesites lunatulus* Öpik, 1975b:34, Pl. 6, Figs 1-4.

*Neopagetina* sp., Rowell et al. 1989, p. 14, Fig. C.

*Pagetides (Discomesites) spinosus* Palmer in Palmer and Rowell, 1995:7, Fig. 7.

#### Material

13 cranidia, 8 pygidia; CPC13176-13179 [Type material of *Discomesites fragum*], CPC13180-13183 [Type material of *Discomesites lunatulus*] and CPC37623-37635 [New topotype material from Site A of Öpik (1975b)].

#### Discussion

The characters that Öpik (1975b) used to differentiate *Discomesites fragum* from *D. lunatulus* can be explained by ontogenetic variation, deformation, preservation or misinterpretation. Öpik's differential characters include: ornamentation, length of the occipital spine, pygidial shape and number of pygidial axial rings.

Öpik (1975b) distinguished *Discomesites fragum* from *D. lunatulus* by its dense granulose ornament; however, this difference is the result of either ontogenetic variation and/or preservation. Firstly, it is important to note that specimens of *D. lunatulus* are considerably smaller than those of *D. fragum*. The type series cranidia of *D. lunatulus* range between 2.6-2.9 mm (n=2) in length (sag.), whereas the type series cranidia of *D. fragum* range between 3.4-4.1 mm (n=3) in length (sag.). This correlation between size and ornamentation can also be observed in pygidia of *Discomesites*. Smaller pygidia (<2.7 mm in length) appear to lack the granulose ornamentation (Fig. 4C-H, J), whereas larger pygidia clearly show dense granulation (Fig. 4A-B, I). It is also worth mentioning that some specimens of *Discomesites* that lack granulose ornamentation, including those of *D. lunatulus*, have a coating of 'desert varnish' (iron oxide), while others appear to have been indurated or partially silicified. It is therefore possible that the difference in ornamentation may have been caused by weathering or diagenesis.

The differentiation of *Discomesites* species

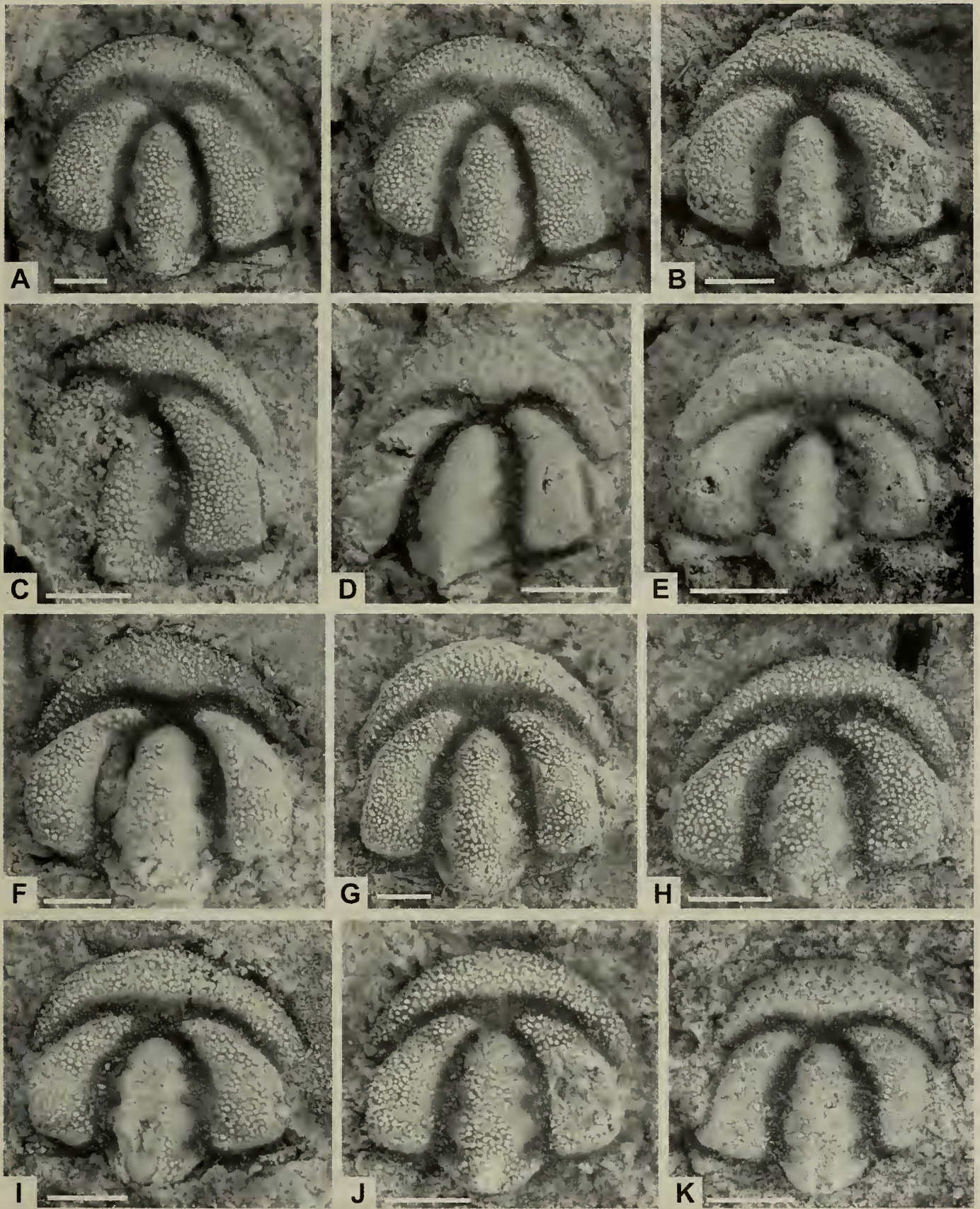


Figure 3. *Pagetides (Discomesites) fragum* Öpik, 1975b. All scale bars = 1 mm. A, CPC13177, holotype cranium, dorsal view, stereo pair; B, CPC13176, cranium, dorsal view; C, CPC13178, latex cast of partial cranium, dorsal view; D, CPC13180, holotype cranium of *Discomesites lunatulus* Öpik, 1975b, dorsal view; E, CPC13181, cranium, dorsal view; F, CPC37623, cranium, dorsal view; G, CPC37627, cranium, dorsal view; H, CPC37628, cranium, dorsal view; I, CPC37632, cranium, dorsal view; J, CPC37635, cranium, dorsal view; K, CPC37629, cranium, dorsal view.

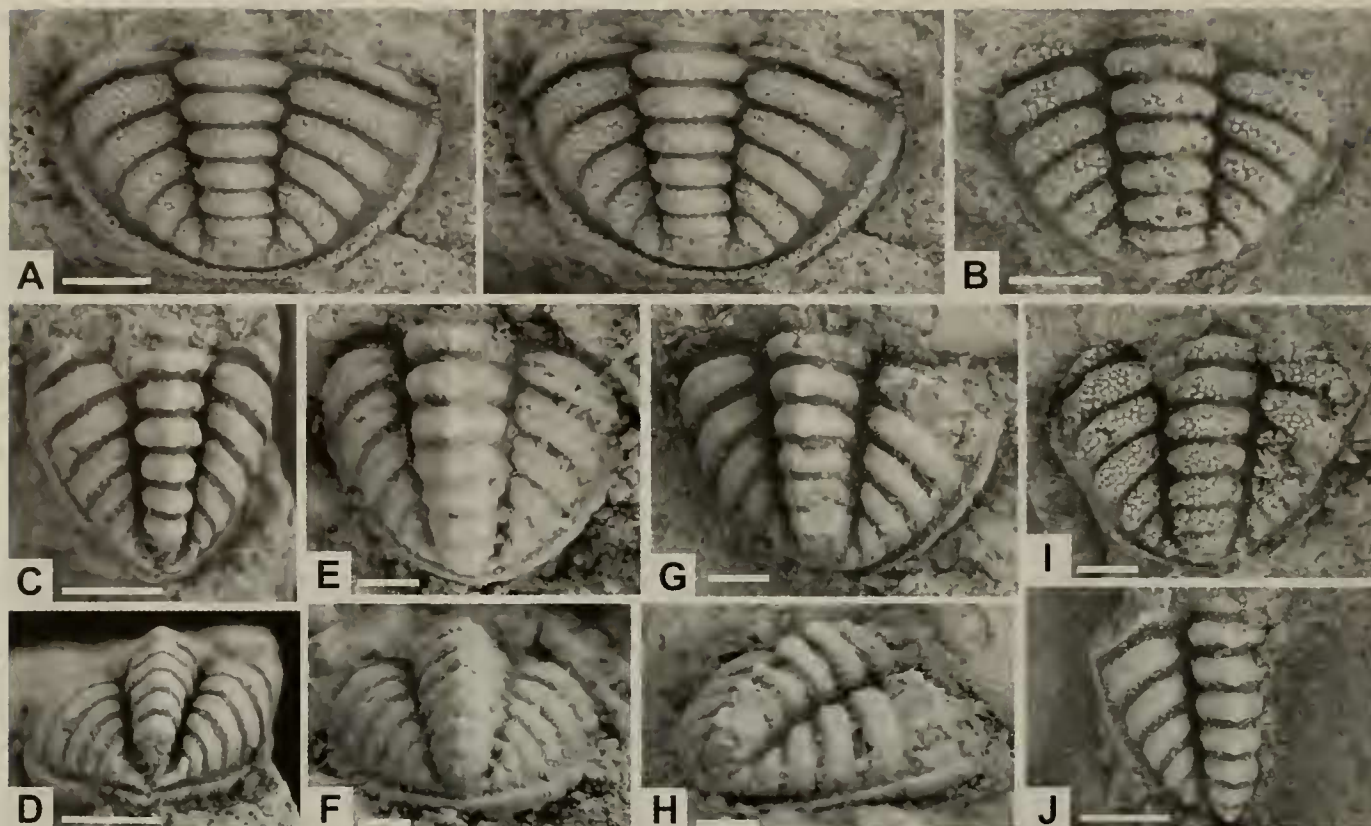


Figure 4. *Pagetides* (*Discomesites*) *fragum* Öpik, 1975b. A, CPC13179, latex cast of pygidium, dorsal view, stereo pair, scale bar = 1 mm; B, CPC37631, pygidium, dorsal view, scale bar = 1 mm; C-D, CPC13182, pygidium, dorsal and posterior views, scale bars = 1 mm; E-F, CPC13183, pygidium, dorsal and posterior views, scale bars = 0.5 mm; G-H, CPC37624, pygidium, dorsal and oblique posterolateral views, scale bars = 0.5 mm; I, CPC37630, pygidium, dorsal view, scale bar = 1 mm; J, CPC37626, partial pygidium, dorsal view, scale bar = 1 mm.

based on occipital spine length appears to have been exaggerated by Öpik (1975b). He described the occipital spine of *D. lunatulus* as 'slender and relatively long'. However, specimens of *Discomesites* that have a preserved occipital spine, including the holotype of *D. fragum*, show no significant difference in size and shape to that of the holotype of *D. lunatulus*. Therefore occipital spine length does not appear to be a reliable diagnostic character.

Pygidial characteristics used by Öpik (1975b) to distinguish species of *Discomesites* can be attributed to preservation or misinterpretation. Öpik (1975b:32) differentiated *D. fragum* from *D. lunatulus* by its 'relatively broad pygidium with six axial annulations', and stated that the latter species possesses seven axial rings. Firstly, tectonic deformation of fossils from the Cymbric Vale Formation is relatively common; see for example, specimens illustrated by Öpik (1975b, Pl. 1, Figs 4-5; Pl. 2, Fig. 1). The larger pygidium of *D. lunatulus* illustrated by Öpik (1975b, Pl. 6, Fig. 3) (see Fig. 4C-D for dorsal and posterior views) has clearly been laterally compressed, thus appears to be narrower (tr.). This was, in fact, noticed by Öpik (1975b:35) in his comments on the illustrated

specimens. Öpik illustrated only two pygidia of *D. lunatulus*, of which only one (CPC13183) has a complete axis preserved. Examination of pygidium CPC13183 reveals the presence of only six distinct axial rings and a terminal piece. It is likely that Öpik misinterpreted the change in slope at the base of the axial node on the terminal piece as an axial furrow. Therefore, based on the evidence above, *D. lunatulus* is herein considered a junior subjective synonym of *D. fragum*.

Palmer (in Palmer and Rowell 1995:7) distinguished the Antarctic species *Discomesites spinosus* from Australian species of *Discomesites* based on the 'presence of axial spines on the thoracic and pygidial segments and of distinct nodes on the pygidial margin'. Examination of Öpik's (1975b) type material of *Discomesites*, in addition to new topotype material from the Cymbric Vale Formation, reveals that smaller pygidia of *Discomesites* (<2.3 mm sagittal length) have axial rings bearing short, median axial nodes or spines (Fig. 4E-H, J). Larger pygidia have less conspicuous axial nodes; in some cases the nodes appear to be absent (Fig. 4A-D, I), implying that axial nodes vary ontogenetically. The



pygidia of *Discomesites spinosus* illustrated by Palmer and Rowell (1995, Fig. 7.2-7.3) conform to this ontogenetic pattern, being less than 2.5 mm in length (sag.).

The presence of marginal nodes opposite the pleural furrows on the pygidium of *Discomesites spinosus* appears to be a rather dubious diagnostic character. Marginal nodes are not clearly delineated on the pygidia illustrated by Palmer and Rowell (1995, Fig. 7.2-7.3). A pygidium of *D. lunatulus* (CPC13183) and an associated unnumbered pygidium display what appear to be faint marginal nodes opposite the pleural furrows. However, this character does not seem to be consistent in all pygidia of *Discomesites* from the Cymbric Vale Formation.

Palmer (in Palmer and Rowell 1995:7) noted that the Australian species of *Discomesites* have 'a slight posterior deflection of the inner margin of the [anterior cranial] border on the axial line'. This is certainly true for the majority of *Discomesites* cranidia from the Cymbric Vale Formation, although there is a great deal of variation, and some cranidia do not display this deflection at all (Fig. 3E, I, J). Therefore, *D. spinosus* is herein considered a junior subjective synonym of *D. fragum*.

Order REDLICHIIA Richter, 1932

Suborder REDLICHIIA Richter, 1932

Superfamily ELLIPSOCEPHALOIDEA Matthew,  
1887

Family ESTAINGIIDAE Öpik, 1975a

Genus ESTAINGIA Pocock, 1964

#### Type species

*Estaingia bilobata* Pocock, 1964, Early Cambrian, Emu Bay Shale, Kangaroo Island, South Australia.

#### Discussion

Jell (in Bengtson et al. 1990:310) originally regarded *Estaingia* and *Zhuxiella* as junior subjective synonyms of *Hsuaspis*. This synonymy was supported in subsequent studies by Palmer and Rowell (1995), Nedin (1995), Jago et al. (1997) and Nedin and Jenkins (1999). Jell (in Bengtson et al. 1990) also suggested that *Strenax* may be regarded as a junior subjective synonym of *Pseudichangia*. Jago et al. (1997) supported Jell in synonymising *Strenax* with *Pseudichangia*, but considered both genera to be junior synonyms of *Hsuaspis*. Recently, Jell (in Jell and Adrain 2003:334) discovered a nomenclatural error between the synonymous genera *Estaingia* and *Hsuaspis*. Jell noted that *Estaingia* should be considered the senior name because the publications

in which the name *Hsuaspis* was first mentioned (Zhang et al. 1957; Zhang 1957) did not satisfy the ICZN criteria for availability, thus *Hsuaspis* must be considered *nomen nudum* in both publications. Therefore *Hsuaspis* became available in Lu et al. (1965), a year after its synonym *Estaingia* was erected by Pocock (1964).

*Estaingia cerastes* (Öpik, 1975b)

Fig. 5A-K

*Strenax cerastes* Öpik, 1975b:14, Pl. 2, Figs 1-6.

*Strenax (Sematiscus) fletcheri* Öpik, 1975b:16, Pl. 3, Figs 1-2.

*Estaingia bilobata* Pocock, Öpik 1975b:11, Pl. 1, Figs 1-7.

*Bergeroniellus* sp., Rowell et al. 1989, p. 14, Fig. A.

*Hsuaspis* cf. *H. bilobata* Pocock, Palmer in Palmer and Rowell 1995:16, Fig. 12.

*Hsuaspis cerastes* (Öpik), Jago et al. 1997:71, Fig. 2B-L, Fig. 3.

#### Material

11 cranidia, 3 librigenae, 5 pygidia; CPC13152-13158 [Öpik's (1975b) illustrated material of *Estaingia bilobata*], CPC13159-13163 [Type material of *Strenax cerastes*], CPC13164 [Holotype cranidium of *Strenax (Sematiscus) fletcheri*] and CPC37636-37641 [New material from Site A of Öpik (1975b)].

#### Discussion

The revision of *Estaingia cerastes* from the Cymbric Vale Formation has been previously documented by Jago et al. (1997) and will only be briefly discussed here. Jago et al. (1997) noted that specimens of *E. bilobata* illustrated by Öpik (1975b) do not belong to this species because Öpik's specimens possess a longer (sag.) glabella (relative to cranial length) and show a marked forward expansion of the glabella, whereas the type cranidia of *E. bilobata* illustrated by Pocock (1964) display a shorter (sag.) glabella that either tapers anteriorly or has a slight waist. Nedin and Jenkins (1999, Fig. 4) have documented the difference in glabella length (or preglabellar field) between specimens of *E. bilobata* and *E. cerastes*. Nedin and Jenkins (1999) have also demonstrated that *E. bilobata* and *E. cerastes* can be differentiated based on cranial length/width ratios. Jago et al. (1997) also suggested that Öpik's specimens of *E. bilobata* and *Strenax cerastes* are likely to represent the same species based on the variation displayed in Öpik's illustrated specimens and those illustrated by Jago et al. (1997). Therefore, in placing *Strenax* in synonymy with *Hsuaspis*, Jago

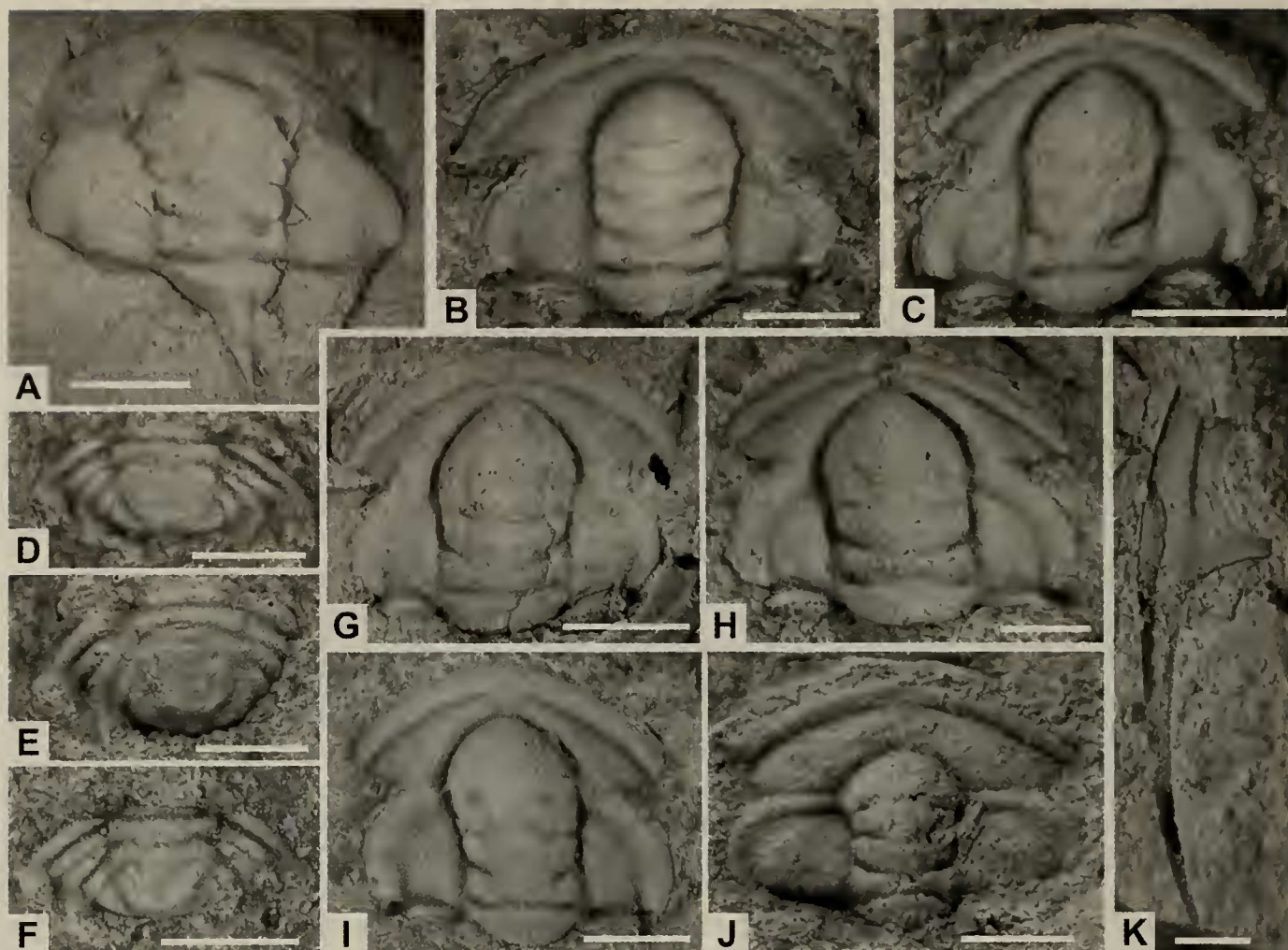


Figure 5. *Estaingia cerastes* (Öpik, 1975b). A, CPC13159, latex cast of holotype cranidium of *Strenax cerastes*, dorsal view, scale bar = 5 mm; B, CPC13152, cranidium, dorsal view, scale bar = 5 mm; C, CPC13156, cranidium, dorsal view, scale bar = 5 mm; D, CPC13157, pygidium, dorsal view, scale bar = 2.5 mm; E, CPC13158, latex cast of pygidium, dorsal view, scale bar = 2.5 mm; F, CPC37638, pygidium, dorsal view, scale bar = 2.5 mm; G, CPC13153, cranidium, dorsal view, scale bar = 5 mm; H, CPC37637, cranidium, dorsal view, scale bar = 2.5 mm; I, CPC37636, cranidium, dorsal view, scale bar = 2.5 mm; J, CPC13164, latex cast of holotype cranidium of *Strenax (Sematiscus) fletcheri*, dorsal view, scale bar = 1 mm; K, CPC37641, librigena, dorsal view, scale bar = 2.5 mm.

et al. (1997) reassigned *E. bilobata* and *S. cerastes* described by Öpik (1975b) from the Cymbric Vale Formation to a single species, *Hsuaspis cerastes*, reassigned herein to *Estaingia cerastes* (Öpik). Jago et al. (1997:71) also noted that the holotype cranidium of *Strenax (Sematiscus) fletcheri* Öpik, 1975b 'is clearly an immature specimen which should not be the basis of a new taxon'. The holotype of *Strenax (Sematiscus) fletcheri* is considered herein a juvenile specimen (sagittal length: 3.0 mm) and junior subjective synonym of *Estaingia cerastes*.

Jago et al. (1997) suggested that specimens of *Hsuaspis* cf. *H. bilobata* described by Palmer (in Palmer and Rowell 1995) from the Shackleton Limestone in the Transantarctic Mountains may belong to *Hsuaspis (=Estaingia) occipitospina*, originally described by Jell (in Bengtson et al. 1990).

Jago et al. (1997:71) based this interpretation on the fact that the Antarctic specimens 'have a glabella of similar length to *H. occipitospina* as well as a similar preglabellar median ridge [= plectrum]'. The Antarctic specimens do appear to have a shorter (sag.) glabella, similar to *E. bilobata* and *E. occipitospina*, compared to that of *E. cerastes*. However, it is important to note that the Antarctic cranidia are considerably smaller (sagittal length: 3.8-5.6 mm) than the large holaspid cranidia of *E. cerastes* (sagittal length: 11-18 mm) illustrated by Öpik (1975b) and Jago et al. (1997). Smaller cranidia of *E. cerastes* (Öpik 1975b, Pl. 3, Figs 1-2; Jago et al. 1997, Fig. 2K) of similar size to the Antarctic cranidia show similar glabella lengths. Therefore the glabella of *E. cerastes* appears to become longer (sag.) relative to the cranidial length during ontogeny; a trend also observed by Jago et al.

(1997:73). This trend is reversed in *E. occipitospina* in that the glabella becomes shorter (sag.) relative to cranial length during ontogeny (Bengtson et al. 1990, Fig. 200). Furthermore, the presence of a plectrum does not appear to be a defining character amongst species of *Estaingia*, since all species possess this feature, including *E. cerastes* (Öpik 1975b, Pl. 1, Fig. 5, Pl. 2, Fig. 5, Pl. 3, Fig. 2; Jago et al. 1997, Figs 2D, E, G, 3B). Jago et al. (1997) also observed that the Antarctic specimens possess an occipital node rather than an occipital spine; however, Jago et al. (1997:71) demonstrated that the occipital spine in *E. cerastes* varies considerably, with some specimens having a small node, while others possess a long, slender spine.

*Estaingia occipitospina* can be further differentiated from *E. cerastes* in having a longer (sag.) anterior cranial border that tapers laterally and the palpebral lobe and eye ridge can be clearly distinguished, with the eye ridge being considerably narrower and of low relief in relation to the palpebral lobe. Specimens of *E. cerastes* and *H. cf. H. bilobata* have an anterior cranial border of approximately equal length (sag., exsag.), and display a palpebral lobe that is continuous with the eye ridge.

Further evidence to suggest that *Estaingia cerastes* and *Hsuaspis cf. H. bilobata* are synonymous can be seen in the morphology of the glabella and pygidium. Although the anterior part of the glabella in the Antarctic specimens is not greatly expanded, the glabella does show a slight expansion anteriorly. This can also be observed in small cranidia, of similar size to the Antarctic specimens, of *E. cerastes* (Öpik 1975b, Pl. 3, Figs 1-2; Jago et al. 1997, Fig. 2K). Based on the description and illustration of the pygidium of *H. cf. H. bilobata* given by Palmer (in Palmer and Rowell 1995:16, Fig. 12.4), there seems to be no apparent difference in the pygidia of *E. cerastes* (Fig. 5D-F; Öpik 1975b, Pl. 1, Figs 6-7). This pygidial similarity was in fact observed by Palmer (in Palmer and Rowell 1995:16), noting that 'all of the pygidial characteristics [of *H. cf. H. bilobata*] are shared with specimens from the Cymbric Vale fauna of New South Wales, Australia, assigned by Öpik (1975b) to *Estaingia bilobata* [= *Estaingia cerastes*]'.

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